THE ANNALS

AND

MAGAZINE OF NATURAL HISTORY.

[SIXTH SERIES.]

No. 15. MARCH 1889.

XVIII.—*Contributions to the Anatomy of the Central Nervous System in* Ceratodus Forsteri. By ALFRED SANDERS, M.R.C.S., F.L.S.

[Plates VIII.-XIII.]

Ceratodus has been known for so short a time that the literature of its nervous system is by no means extensive; three memoirs exhaust the list of those that refer to that subject—one by Prof. Huxley *, another by Beauregard †, and a third by Prof. Burt. G. Wilder ‡, to which may be added two others which touch only slightly or not at all on the nervous system; these are a very full account of the anatomy of *Ceratodus* by Dr. Günther §, a memoir which first introduced the animal to the notice of scientific men, and another, more recent, by H. Ayers ||, which goes more into the microscopic anatomy.

* "Contributions to Morphology. Ichthyopsida.—No. 1. On *Ceratodus Forsteri*," Proc. Zool. Soc. 1876.

† "Encéphale et Nerfs Craniens du *Ceratodus Forsteri*," Journ. de l'Anatomie et Phys., Ch. Robin and G. Pouchet, 1881.

‡ "The Dipnoan Brain, *Ceratodus*," American Naturalist, vol. xxi. 1887.

§ Phil. Trans. Roy. Soc. 1871.

|| "Beiträge z. Anatomie und Physiologie d. Dipnoer," Jenaische Zeitschrift f. Naturwissenschaft, Bd. xviii.

There are a few memoirs which treat of the brain of *Protopterus* or *Lepidosiren* which will be referred to in the course of this paper.

The specimens on which the present paper is founded were caught under my immediate supervision in the River Burnett at Gayndah, in Queensland, Australia.

The treatment to which the nervous system was subjected was applied before molecular death could take place.

This treatment consists in placing the head immediately after it has been cut off into Müller's solution to which spirits of wine has been added in the proportion of one third; the solution is changed next day and again two or three times in the course of three weeks: the skull containing the brain is then placed in a 2-per-cent. solution of potassium bichromate, which is changed about once a fortnight, until the brain becomes sufficiently hard to be sectioned; this occurs at various periods, taking a shorter time in the higher Vertebrates than in the lower; in the present case the period extended to more than twelve months.

The best staining-fluid, I find, is an aqueous solution of the aniline dye known commercially as soluble blue.

This method may seem antiquated to some people, who think everything new must be best; but I have always found it to succeed well, and it is of great advantage to persons situated as I was, who are not in a position to attend to cutting sections for some time after the capture of the animals; in fact I can recommend it as an all-round method for travellers, and in cases where the material is too precious to be wasted on experiments it is better than most of the new ones, which although perhaps for minute points they may be good, yet are more or less uncertain, and are therefore not suited for use in the bush.

The chromo-silver method of Golgi, for instance, as given in Fridtjof Nansen's memoir *, is excellent for showing cell-processes of the brain in the higher Vertebrates, but requires more civilized surroundings than are to be found in that sort of place for its proper carrying out.

Macroscopic Anatomy.

General Description.

The brain (Pl. VIII. fig. 2) on its ventral side accurately fits into a depression in the base of the skull; but on the

* 'The Structure and Combination of the Histological Elements of the Central Nervous System:' Bergens Museum, 1886.

dorsal side the cranial cavity is much larger, so that there is a considerable space between the walls of the cranium and the surface of the cerebro-spinal centres; this is filled by a coarse and loose network of connective tissue, the trabeculæ of which carry vessels and capillaries; this arrangement resembles that of *Protopterus*, and, as Wiedersheim * remarks, may possibly serve to secrete the subarachnoid fluid.

A thick membrane of great toughness encloses the brain and spinal cord; but towards the posterior end of the latter it becomes thinner and more membranous.

Two glandular bodies are developed in connexion with this pia mater, as it may be called, it evidently corresponding to that structure, at least in position. The posterior body, of a spongy character, forms a cover to the sinus rhomboidalis, or fourth ventricle, resembling that of *Petromyzon* as described by Ahlborn †. It closes the whole ventricle with the exception of a small opening at the posterior end, in this respect resembling the corresponding structure in Plagiostomata; its structure is not so much vascular as of a glandular nature, being composed of a congeries of tubules which appear to connect an upper and lower plate; externally the whole is connected with and passes into the tough pia mater enveloping the medulla oblongata, which is continuous with the membrane that encloses the remainder of the brain.

The anterior body, which Beauregard ‡ mistook for nervous tissue, resembles the cover of the fourth ventricle in structure, inasmuch as its tissue is made up of tubules, but differs in the fact that these tubules are more contorted; it enters the third ventricle, forming a spongy mass, termed by Prof. Huxley § the tela vasculosa, but in which I failed to discover any capillaries, its structure being entirely glandular.

This spongy mass (Pl. IX. fig. 5) extends to the anterior end of the cerebrum, separating the dorsal wall of one side from that of the other, so that the lateral ventricles are not closed in above by nervous tissue. At the anterior end of the cerebrum the lower surface of this structure is connected by a lamina of connective tissue which passes between the inferior internal fold of the cerebrum to join the general covering of pia mater at the inferior surface of the brain. This fold is

* 'Morphologische Studien:' Jena, 1880, p. 73. Also Jenaische Zeitschr. Bd. xiv. (1880).

† Zeitschr. f. wiss. Zool. Bd. xxxix. (1883).

‡ *L. c.* p. 232.

§ *L. c.* p. 29.

termed the "Falx" by Prof. Burt. G. Wilder *, who was not certain that it was continuous with the lower surface of the tela choroidea. The ventricular partition is thus seen to be made up for a great part of its extent by tissue which is not nervous. The function of these two bodies is probably, as Wiedersheim † suggests in *Protopterus*, also in this case, for the purpose of secreting the cerebro-spinal fluid.

Over the third ventricle the pia mater forms a sort of conical membranous cap, in the summit of which is found a body, the pineal gland; but this shows no retinal structure, even in the modified form described by Ahlborn in *Petromyzon*, much less the comparatively high development described by Spencer ‡ in Lacertilia and by Graaf § in *Anguis fragilis*. This cover resembles that in *Protopterus* ‖, but it extends much higher in *Ceratodus*; in *Lepidosteus* also a membrane resembling this is described by Balfour and Parker ¶, but this latter appears to resemble more *Protopterus* than *Ceratodus* in appearance. In *Rhina squatina* and *Acanthias vulgaris* also there is a membranous cover to the thalamencephalon, which seems to be a homologous structure.

The pia mater is more closely attached to the rhinencephalon than to the remainder of the brain, where it can be easily stripped off with a pair of forceps. On the ventral surface (Pl. XI. fig. 15) of the medulla oblongata and the commencing spinal cord, immediately in front of the entrance of the anterior root of the trifacial nerve, the anterior median fissure is filled up with a development of the pia mater of a semicartilaginous consistence; it is not, however, by any means of the structure of cartilage, but consists of thick, round, smooth fibres, several of which join together into one at the external edge in a transverse direction, forming a sort of fenestrated structure, whereby it becomes thicker in the central line and thins off exteriorly, where it joins the ordinary membrane; it appears to act as an elastic pad which would protect the medulla oblongata from sudden shock; but why the other parts of the brain should not be as well protected does not appear.

Like *Protopterus*, *Ceratodus* presents a wide and well-developed medulla oblongata connected by a narrow mesencephalon and thalamencephalon with the prosencephalon; but there is no sudden angle between the former and the latter as is described by Wiedersheim ** in *Protopterus*.

* *L. c.* p. 546.
† *L. c.* p. 71.
‡ Quart. Journ. Micr. Sci. 1886.
§ Zool. Anzeiger, March 1886.
‖ Wiedersheim, *l. c.* p. 71, fig. 21.
¶ Phil. Trans. 1882.
** *L. c.* p. 70.

When the pia mater is stripped from the prosencephalon, the nervous tissue that remains is not of any great amount; it forms a pair of thin plates, each folded so as to form the outer walls and the lower part of the inner walls of two imperfect lateral ventricles, which, as above said, are completed by the tela choroidea. I look upon them as lateral ventricles, notwithstanding that their walls are not completed by nervous tissue; but if it is considered essential to the connotation that the nervous walls should be complete, then of course the term ventriculus communis should be applied. The chamber thus formed is elongated from before backward, but is narrow from side to side in its dorsal part; anteriorly it communicates with the ventricle of the olfactory lobe by a foramen passing through the neck of the same. Beauregard * supposed that the anterior part of the prosencephalon belonged to the rhinencephalon; but microscopic examination shows that it has the same structure as that of the remainder of the cerebrum.

Below, this chamber communicates with an expanded bulla by a large oval opening extending for the whole length of the cerebrum; the inner wall of this bulla is in contact with that of the other side, but separated by a layer of pia mater, and is only attached behind by a very small transverse commissure.

The prosencephalon in *Ceratodus* differs from that of *Protopterus* in the incompleteness of the nervous tissue of the walls †, but agrees in the hemispheres being entirely separable except for the above-mentioned narrow transverse commissure, which in *Protopterus* runs between the two crura cerebri, but in *Ceratodus* between the posterior ends of the cerebrum itself. The latter also differs in the greater development of the rhinencephalon, which in Wiedersheim's figures is not shown, but which Fulliquet ‡ by transverse sections demonstrated to be present indeed, but small and scarcely separable from the cerebrum.

The thalamencephalon is a deep trough, open above, where pia mater alone closes it. It is wider in front, where it communicates with the lateral ventricles by a broad opening, which is divided into two by the tela choroidea, narrower behind, where it passes into the aqueduct of Sylvius by a foramen nearly as large as the ventricle of the optic lobe; above this latter opening is situated the posterior commissure, which is not visible by the naked eye, but is shown in the microsco-

* *L. c.* p. 231.

† Wiedersheim, *l. c.* p. 70.

‡ "Recherches sur le cerveau du *Protopterus annectens*," Recueil Zoologique Suisse, tome iii. (1886).

pical sections; on the posterior end of the walls, immediately in front of the point where they merge into the optic lobe, there is a tuberosity which transverse sections demonstrate to be double (Pl. IX. fig. 5); these tuberosities form the ganglion habenulæ, which corresponds to the tuberculum intermedium of Teleostei and Plagiostomata.

Fulliquet in his detailed description of the brain of *Protopterus annectens* mentions two tuberosities in a corresponding position which much resemble these. He considers that they form part of the epiphysis. This surely must be a misapprehension; they might be, and probably are, remains of the ganglion which supplied that sense-organ, but they could not be part of that sense-organ itself.

On the floor of the thalamencephalon there is visible anteriorly the projecting cord of the commissure of the two hemispheres, which corresponds to the anterior commissure; behind this is an opening leading into the infundibulum.

The pituitary body or hypophysis is a large and extensive structure formed apparently of glandular tissue composed of interlacing tubules; it seems to be much larger here than in *Protopterus*.

No part of the chiasma nervorum opticorum is visible externally, but on removal of the pia mater the optic tract is distinctly seen passing upward and backward to the summit of the optic lobe; this is much more visible in brains preserved in potassium bichromate than in spirit preparations.

The mesencephalon is a paired tuberosity, small and narrow, and does not present that external transverse striation, visible presumably to the naked eye, given in fig. 20, taf. iii. of Wiedersheim's paper. Fulliquet* lays great stress on the fact that in *Protopterus annectens* the mesencephalon is single; he considers that this indicates a low degree of development, the original single state of this segment of the encephalon being preserved.

Although the cerebellum is not well developed, being merely a bridge crossing the anterior end of the sinus rhomboidalis, yet it appears to exceed that of *Protopterus* in size; internally it presents a longitudinal ridge, which dwindles away posteriorly; externally the position of this ridge is indicated by a median longitudinal furrow; posteriorly it terminates in a free edge.

The sinus rhomboidalis is a broad shallow trough which diminishes posteriorly rather suddenly; its widest part is just behind the crura cerebelli. The floor is flat, and in the central

* *L. c.* p. 20.

line two longitudinal ridges, separated from each other by a median longitudinal furrow, are faintly visible; at the anterior end two other longitudinal ridges appear, which contain the ganglion of origin of the anterior root of the trifacial. These two pairs of ridges pass beneath the cerebellum, and the central ones are traceable into the aqueduct of Sylvius. Posteriorly this ventricle passes by a long funnel-shaped passage into the central canal of the corda spinalis.

Apparent Origin of the Cranial Nerves.

Second pair (Pl. VIII. fig. 1, *n.* 2).—The optic nerves, which are of small size, pass after a long course each through a foramen which appears to correspond to the optic foramen. Each one is closely attached for a short distance to the first branch of the trifacial nerve; but it is possible to separate them by dissection without injury to either. The nerve, then passing between the origins of the eye-muscles, enters the eyeball.

Third pair (Pl. VIII. fig. 1, *n.* 3).—The oculomotor arises in the usual position at the base of the optic lobe in what Ahlborn terms the epichordal part of the brain, and passing out of the brain through its special foramen, it immediately enters the sheath of the first branch of the trifacial, from which it cannot be dissected without injury; after a short distance it abandons its companion, and, taking an independent course, can be traced to the muscles of the eyeball. In *Protopterus* Wiedersheim was uncertain about the origin of the corresponding nerve, thinking it might be a branch of the trifacial. Fulliquet *, however, found its origin in the usual position, but supposed that the first branch of the trifacial shared its distribution; if this should be the case in *Protopterus* it certainly is not so in *Ceratodus*, although of course in the latter case there may be an interchange of fibres. Serres † absolutely denies the existence of this nerve in *Protopterus*, as also of the fourth and sixth.

Fourth pair.—The trochleares are too small to be seen in a macroscopic dissection, which justifies Serres in denying their existence; but when we come to the microscopic description it will be seen that their presence is demonstrable in the transverse section of the part between the optic lobes and the cerebellum, where their decussation and emergence from the brain are distinctly to be seen (Pl. XI. fig. 9).

Fifth pair.—Trifacial arises by two roots immediately behind the junction between the cerebellum and the restiform

* *L. c.* p. 30. † Compt. Rend. 1863, p. 579.

bodies; the anterior is the largest; on it the gasserian ganglion is developed, after passing through which it joins the posterior root, which arises a short distance behind the anterior root, and immediately divides into two branches, which join the anterior root just beyond the ganglion.

The branches of the trifacial in *Ceratodus* do not exactly correspond to those of this nerve in Mammalia, but seem to be more generalized, and the distribution of the various trunks appears to be interchanged to some extent.

The first branch, which may be looked upon as the ophthalmic, is given off from the anterior root before its junction with the two branches of the posterior root. It passes out of the skull through a special foramen into a fossa, which is occupied by the temporal muscle and which is not divided from the orbit; it passes forward closely applied to the outside of the skull, where it is joined by the oculomotor nerve, as already mentioned; it then passes round a process of the bone named by Prof. Huxley the pterygo-palatine to the outer side of the olfactory lobe; it then crosses the olfactory sac, immediately in front of its connexion with the olfactory lobe, to the outer edge of the cartilage dividing the two olfactory sacs and lobes from each other, which is termed by the same authority the mesethmoid cartilage; it then passes forward between the olfactory sac and this cartilage, and finally dividing into two branches, is distributed to the external skin of the central portion of the upper lip.

The posterior root (Pl. VIII. fig. 1, *co.*) gives off close to the junction of its two branches with the anterior root a communicating branch to the vagus; this curves round through the outer wall of the ear-capsule, external to the semicircular canals, and joins the vagus just beyond where the branchial nerves and the visceral branch are given off, so that it only joins the ramus lateralis; it thus differs from the *Lepidosiren paradoxa*, in which, according to Hyrtl *, the communicating branch joins the ganglion of the vagus, whereas here it effects a junction beyond it.

The junction between the anterior and posterior roots of the trifacial takes place in a slightly different manner on the two sides; on the right side the whole of both roots join at once, on the left side there is a supplementary junction in the shape of a short branch from the posterior root which joins the anterior root at some distance along its course.

The nerve (Pl. VIII. fig. 1, *m.*) resulting from this junction may be looked upon as the combined superior and inferior maxillary; it divides into two branches, an external and an

* Abhandl. d. königl. böhmisch. Gesellsch. d. Wiss. Bd. iii. (1843–4).

internal branch; at the anterior border of the temporalis muscle both these give off twigs to the floor of the orbit; the external branch then goes forward over the membranous bag which is situated above the side of the mouth. This bag has no communication with the olfactory vestibule, on the outside of which it is placed, but opens externally behind the angle of the mouth through a special aperture. The nerve ultimately divides into two branches, each of which gives off terminal filaments in a fan-like manner, which are distributed to the deep side of the upper lip, external to the termination of the ophthalmic branch.

The internal division takes a turn inward and divides into two branches; the first goes directly downward and enters the upper border of the mandible, in front of the origin of the temporalis muscle; the second, which may be looked upon as the palatine nerve, passing beneath the ophthalmic, plunges downward immediately in front of the pterygo-palatine bone, and is distributed to the pad of mucous membrane situated on the roof of the mouth.

Sixth pair.—The abducens was not found in any of these specimens.

Seventh pair (Pl. VIII. fig. 1, *n.* 7.).—The facial arises immediately ventrad of the origin of the posterior root of the trifacial; it has a single root, which does not join either the fifth in front or the acusticus behind, as is the case in *Protopterus* *, in which also, according to Fulliquet, it has two roots, but passes directly outward through the mass of cartilage on the outer side of the ear-capsule, which is probably the petrosal; it terminates by being distributed to the integument outside and in front of the branchial chamber; close to its origin it gives off from its under surface a branch which plunges down in the cartilage at the base of the skull and divides into a pair of trunks—one, passing forward through the base of the skull beneath the brain, eventually supplies the anterior part of the roof of the mouth, inside and between the olfactory sacs; the other passes back and supplies the middle and outer part of the anterior wall of the branchial chamber.

Eighth pair (Pl. VIII. fig. 1, *n.* 8).—The acusticus arises by one root behind and beneath the trifacial, in close contact with the origin of the facial; its root emerges obliquely. At its origin the anterior margin is slightly higher on the left side and slightly lower on the right than that of the facial; but its posterior margin is on the same level on both sides. There is no accessory acusticus to be found here as is the case in *Protopterus*. This nerve divides into two main trunks,

* Wiedersheim, *l. c.* p. 75, fig. 19.

which are distributed on the inferior surface of the otic vesicle, one branch going to the external, the other to the internal division of that vesicle.

Ninth pair.—The glossopharyngeal has not a distinct and independent root in *Ceratodus*, but is a branch of the vagus, and will be described with that nerve.

Tenth pair (Pl. VIII. fig. 1, *n.* 10).—The vagus arises by five contiguous roots on the right side and by four on the left; the outer and anterior root is the largest in both cases.

The first branch is given off at right angles to the course of the nerve and is the glossopharyngeal; after a short course this branch enlarges into a ganglion, the distal end of which is the broader; from this ganglion three branches are given off. The most anterior, which is the largest, plunges down in front of the branchial chamber and supplies the membrane lining the anterior wall of that chamber; the middle branch is supplied to the membrane between the first branchial arch and the anterior wall of the branchial chamber; the third branch runs along the first branchial arch between the two lamellæ of the branchiæ to the ventral surface, where its terminating branches are distributed to the pharynx.

A short distance behind the glossopharyngeal a large ganglion is attached to the inferior surface of the main trunk of the vagus (Pl. VIII. fig. 1, *gn. v.*); this ganglion ends in three expansions, having first given off a small communicating nerve to the glossopharyngeal; the three terminating ganglia supply branches to the membrane closing the spaces between the branchial arches, and each gives off a nerve (Pl. VIII. fig. 1, *b.*) which runs in a groove at the base of the branchiæ to the ventral side, where it terminates in the same way as the branchial branches of the glossopharyngeal. In addition, the third swelling gives off a large nerve, which passes on behind the branchial chamber and becomes the visceral branch of the vagus.

The main continuation of the nerve, after giving off the above-mentioned ganglion, passes backward along the side of the vertebral column as the ramus lateralis (Pl. VIII. fig. 1, *r. l.*).

The origin of the vagus, as thus described, differs considerably from that of the corresponding nerve of *Protopterus**, in which it arises by both dorsal and ventral roots, which all end in the ganglion, the consequence being that none of the branches are independent of that body.

Two nerves arise from the ventral side of the posterior end of the fourth ventricle behind the vagus; they originate like

* Wiedersheim, *l. c.*

the ventral roots of the spinal nerves, except that they have two contiguous roots instead of one, which shows that each one ought to be counted as two. They have no dorsal roots, and take a long course in the vertebral canal before passing out through their respective foramina, which are high up in the vertebral arches on the same level as the foramina through which the dorsal roots of the succeeding spinal nerves emerge.

It is possible that they may correspond to the two ventral roots of the vagus, as described by Wiedersheim*, but here they certainly do not join the vagus. They cannot be looked upon as the hypoglossal, as the course usually followed by that nerve in fishes is here pursued by the second and third spinal nerves; their course outside the skull was not made out, but it is improbable that they would join those nerves, as the intervening trunk, which is the first spinal nerve, does not do so.

The ganglion (Pl. VIII. fig. 1, *sp. gn.*) of the spinal nerves forms an angle in the cartilage of the vertebral arch, and extending down near the outer edge to the level of the floor of the vertebral canal, it is there joined by the ventral root, which has itself passed through a distinct foramen.

The hypoglossal appears to be represented by the second and third spinal nerves, which pass into and supply the anterior fin.

Central Cavities.

The central canal (Pl. XI. fig. 15, *c. ca.*) in the spinal cord is rather large comparatively speaking; its long diameter is placed from side to side and it is compressed from above downward. In its progress forward the canal gradually widens, the lateral ends become pointed by degrees, and on approaching the posterior end of the fourth ventricle the sharp angle formed by these pointed extremities slightly turns downward. At this point the canal is a large and extensive channel occupying about one third of the extent of the section; the floor is convex and the roof is vaulted. A short distance in front of this region a depression or notch appears in the roof, which is attached to the dorsal edge of the section by a plug of connective tissue separating one side from the other; this depression increases as the canal deepens, until finally the fourth ventricle or sinus rhomboidalis opens out; the walls recede, the floor becomes wider, and the section enlarges in every direction—an enlargement due partly to the

* *L. c.* p. 76, fig. 19.

increase of the parenchyma, but principally to the expansion of the lumen.

The posterior part of the floor of the fourth ventricle presents the same form as that of the anterior part of the funnel-shaped termination of the central canal, except that at the lateral part the junction of the floor with the walls is more rounded and less sharp than further back.

The two multiaxial fibres, a description of which will be given presently, form a couple of ridges projecting into the floor; between the two there is a depression, and again on each side another leading to the lateral parietes, which are here perpendicular. Further forward the two prominences become higher and more marked, and contain not only the multiaxial fibres but also some of the fibres of the ventral columns; they correspond to the longitudinal ridges which are seen on the floor of the sinus rhomboidalis in the Plagiostomata.

In the wall of the ventricle there now appear two tuberosities, one forming a club-shaped dorsal termination, like a coping to a wall, which belongs to the trifacial (Pl. X. fig. 13, *v. tri.*), the other situated lower down, just above the junction with the floor; towards the posterior end this is a long, low, flat swelling (Pl. XII. fig. 14, *ff.*), but further forward it gradually sinks down until it becomes a small rounded eminence; this corresponds to the bead-like tubercles on the floor of this ventricle in *Scyllium*, although it is here a ridge and not discrete formations.

The fourth ventricle passes beneath the cerebellum without any diminution in size (Pl. X. fig. 11); on the contrary, it gradually widens from behind forward; at this part a low broad tuberosity belonging to the trifacial is visible. Towards the anterior end of the cerebellum (Pl. XIII. fig. 10) this swelling disappears and the depression between the ventral columns loses its gentle contour and becomes a triangular trough, with the sides meeting at an angle at the bottom; here the lumen is more contracted, and its space is diminished by the projection of a process from the roof of the cerebellum.

In the ventricle (Pl. XI. fig. 9) of the mesencephalon or aqueduct of Sylvius the floor gradually deepens into a narrow fissure, which eventually opens into the infundibulum; in addition to the fissure in the floor of the optic lobe there is one in the roof which extends for the whole length of the lobe.

In the region of the anterior end of the optic lobe an offshoot of the fissure on the floor is observed to be directed backward; this can be traced beneath the floor of the optic ventricle for some distance, and ends in a *cul-de-sac* immediately in front of the point where the infundibulum detaches itself from the under surface of the brain to pass down to the hypophysis.

From the point where the ventricle of the optic lobe joins the infundibulum the latter proceeds obliquely both upwards and downwards, upwards through a membranous tube to the epiphysis and downwards to the hypophysis; at the point of junction with this body the pia mater splits into two layers, one going to envelop the hypophysis, while the other passes over to the opposite side and shuts in the lower end of the infundibulum, so that there is no actual communication between this passage and the cavity of the hypophysis, as is the case in *Scyllium*; neither is this passage completed by nervous tissue, but the lower end is closed merely by this membrane.

Anteriorly the third ventricle communicates by means of a ventriculus communis with the two lateral ventricles in the cerebrum, the walls of which are completed by the tela choroidea; each of these again communicates anteriorly with a ventricle in the olfactory lobe.

Microscopic Anatomy of the Brain.

Cerebrum.

On inspecting a section through the dorsal wall of the cerebrum (Pl. XIII. fig. 22) it is possible to make out four layers counting from the surface turned toward the ventricle, which is lined by an endothelium continuous with that of the remainder of the cavities of the brain. The cells of this endothelium send processes into the parenchyma of the cerebrum, and carry on their internal surface a flat disk, which, with those of the contiguous cells, form a membrane which lines the ventricle and in some places shows the remains of cilia.

The most internal of the four layers of the parenchyma of the cerebrum consists of cells which occupy about one quarter (more or less) of the thickness of the cerebral wall.

External to these cells the second layer, composed of a finely granular neuroglia, occupies rather more than one fourth of the total thickness.

The third layer consists of cells larger but much less numerous than those of the first layer.

The fourth or external layer is occupied by a zone of granular neuroglia, which extends to nearly half of the total thickness, filling the space between the third layer and the outer edge.

These measurements are approximative only and vary somewhat in different parts of the cerebrum.

The cells of the inner layer are generally spherical in shape, but some oval and pyriform ones are also met with and even occasionally fusiform ones are seen. They range in size from 0·0084 millim. to 13 μ in diameter; they show a peculiar tendency to become vacuolated, in which state they resemble the appearance presented by Infusoria when too much compressed; this vacuolation is caused probably by the preservative fluid not penetrating with sufficient quickness through the parenchyma, as it is only found in those cells which occupy the internal surface. When the cells are in this state the nucleus and the nucleolus are obscured; but in the normal cells they are quite distinct. These cells are closely crowded together and give off processes which join the fibrillar network of the neuroglia with which they are surrounded.

In the second layer the fibrils permeating the neuroglia of which it is composed have a decidedly longitudinal direction and are probably continuations of the fibres of the crura cerebri.

The cells of the third layer are on an average of a larger size than those of the first or internal layer; they range from 17 μ long and 14 μ wide to 30 μ long and 12 μ wide; they are not so closely packed together, but are rather sparsely scattered along the zone which they occupy; they usually give off two or three thick processes instead of numerous fine ones; they resemble the larger cells in the cerebrum of the Teleostei.

In some places the first or internal layer extends through the parenchyma of the second layer and becomes continuous with the third, so that the intervening neuroglia loses its distinct individuality and the three layers merge into one.

The fourth or external layer is entirely or very nearly devoid of cells, and consists of a fine fibrillar network imbedded in a finely granular neuroglia, having the usual characters and showing a slight tendency to radial striation.

The palissade cells of the external surface are very slightly developed and are scarcely perceptible; yet when they do occur they send processes into the interior, as in Plagiostomata and Teleostei.

The above-described arrangement occurs in the dorsal wall of the cerebrum. The ventral parietes forming the bullæ offer a slightly varying disposition of the elements of the nervous substance. Here the central layer of cells is absent, and only two layers are observable—one internal, composed of cells altogether resembling those which form the internal layer in the dorsal walls; the other, made up of the ordinary neuroglia, extends to the outer surface; the line of demarcation between these two layers is irregular; sometimes isolated portions of neuroglia penetrate into the stratum of cells, and on the other hand groups of cells project into the neuroglia; the cells are arranged more loosely in some parts, in other places they appear to be more closely packed together. The stratum of neuroglia varies in width from one third to nearly one half of the thickness of the walls, the remainder of the space being occupied by the cells.

Lobi olfactorii.

In the structure of the olfactory lobes (Pl. XIII. fig. 21) one may distinguish four layers interposed between the endothelium, which lines the very large ventricles and which is continuous with that of the cerebrum, and the external surface.

Internally is seen a layer of cells resembling in every respect those of the inner layer of the cerebrum, with which they are continuous; their measurements also are very much about the same; they vary in diameter from 10 μ to 0 0145 millim.

External to this layer of cells is a space occupied by a finely granular neuroglia, in which a fibrillar network is found having a general longitudinal direction. Longitudinal fibres of a larger size occur scattered through this layer; these are in some places collected into a bundle immediately internal to the outer layer; these fibres have fusiform cells developed along their course, which cells are of a larger size than those of the inner layer; their size varies from 0·0259 millim. long and 0·0125 broad to 12 μ long and 0·0098 millim. broad; they follow the curves of the ventricle, so that they sometimes become visible in a transverse section, as in the figure.

As Fritsch has justly remarked, the glomeruli are as characteristic of the olfactory lobes as the Purkinje cells are of the cerebellum; they occupy the external part of the lobe in *Ceratodus*, as in Plagiostomata and Teleostei, and they present the same sort of structure. The fibrils which proceed from them constitute an external layer, which ultimately contributes to form the olfactory nerves.

At the anterior end of the ventricle there is a corresponding arrangement of the layers from behind forward, so that they surround the ventricle in concentric strata. Anteriorly the fibrils of the second layer form a distinct bundle, the outer fibrils of which go to a group of glomeruli situated in the centre of the anterior wall of the ventricle, while the inner fibrils pass over to the other side.

On comparing a section through the olfactory lobe with one through the cerebrum, it is possible to imagine how the former could have been evolved from the latter. The internal layer of the olfactory lobe resembles in every respect and is continuous with the internal layer of the cerebrum, the second and third layers of which would correspond to the middle layer of the olfactory lobe, while the glomeruli would be the condensed external layer of the cerebrum.

This idea is supported by the fact that the three internal strata of the cerebrum equal in width the two internal layers of the olfactory lobe, while the external layer of the former is much wider than the zone of glomeruli, which are undoubtedly formed of more condensed substance than the neuroglia of the cerebrum.

Hypoaria.

The hypoaria (Pl. IX. fig. 6) as distinct structures seem to be represented in *Ceratodus* only by the laminæ of nervous tissue which form the walls of the infundibulum.

Their structure resembles that of the cerebrum, that is to say, there exists a layer of cells on the inner surface, and external to this the parenchyma is occupied by neuroglia, in which a fine network of fibrillæ is imbedded.

The larger cells which characterize the third layer of the cerebral walls are here absent.

Lobi optici.

The optic lobes (Pl. XII. fig. 8, Pl. XIII. fig. 23) have a structure comparable to that of the optic lobes of the Plagiostomata. On the internal surface there is seen the layer of endothelial cells which line the aqueduct of Sylvius and are continuous with the endothelium of the remaining cavities of the brain.

External to the endothelium four layers may be distinguished in this structure.

The first is a layer of cells the great majority of which are spherical, but many are pyriform or oval; each sends a process from one side in a radial direction, which may be traced into the parenchyma of the interior of the lobe; the cells in this layer show a tendency to be arranged in clusters on these radial processes, in the same way as in the corresponding layer of the tectum lobi optici in Teleostei, but the arrangement is not so well marked here; many of them resemble the cells of the internal layer of the cerebrum. Their size is about 16 μ in diameter.

Placed externally to these cells there is a zone of transverse fibrils which, proceeding upward, eventually collect into the transverse commissure on the dorsal part, to be mentioned presently; they are derived from fibres coming forward from the region about the floor of the ventricle, being originally derived from the lateral columns of the cord.

These two layers occupy about half the thickness of the section; many cells of the same size or larger than those of the first layer are seen to be scattered throughout this part, and, in addition, fusiform cells are to be found which are placed, some in a radial, others in a transverse, direction; the latter give a process from each end which joins the transverse fibrils; from the former processes run out to join the radial fibrils, which are visible traversing this stratum from the internal layer; these radial cells in some cases may be observed to give off from one end a comparatively broad process going towards the inner margin of the lobe, and from the other end of the cell a fine process which goes towards the outer surface and is soon lost in the parenchyma.

These cells measure from 28 μ to 32 μ in length and from 10 μ to 15 μ in breadth.

The third layer, counting from the internal surface, has a smooth, finely granular neuroglia, in which an extremely minute radial striation can be detected; it occupies about half the remainder of the section.

The fourth or external layer consists principally of longitudinal fibrils, which are the continuation of the fibres of the optic tract; in this zone a few cells are very sparsely scattered. The neuroglia in which these fibrils and cells are imbedded is coarser than that of the third layer and is permeated by a fibrillar network.

In the central line of the roof, close to the dorsal surface, there is a transverse commissure, formed of very fine fibrils, which are derived from the second layer of the optic lobe above described; it corresponds to the transverse commissure in the tectum lobi optici of Teleostei and the optic lobe of Plagiostomata.

Precisely in the region where this commissure occurs there is a ganglion of large cells (Pl. XII. fig. 8, *t. c. op.*), which corresponds to the roof-ganglion of Plagiostomata ("Dach-Kerne" of German authors). The greater number of these cells are in close apposition to the endothelium which lines the fissure present in the roof of the optic lobe; but a few are placed with their broad ends contiguous to the outer surface.

They are usually pyriform, having a process emerging from the pointed end, which process is directed radially, *i. e.* towards the inner surface, thus differing from the corresponding cells in the Plagiostomata, where the corresponding cells send processes in a transverse direction towards the outer side. There also occur others which have a fusiform shape; these send a process from each end, one being larger than the other. The fusiform specimens are found in the part of the ganglion which is situated close to the inner edge, while the pyriform ones are found near the outer edge. Their size varies between 82 μ long by 4 μ broad and 60 μ long by 5 μ broad.

These cells resemble the cells of the ventral ganglion of the spinal cord as to the nuclei and nucleoli, though differing much in shape. The nuclei are more deeply stained than the cell-contents, and the nucleoli have a clear space round them. Occasionally these cells exhibit two nucleoli, which are situated a short distance apart; in this case the clear space is single but elongated in shape, and meanwhile the nucleus remains unaffected; whether these were cases of cell-division I could not determine, the staining-fluid employed not showing any pattern of karyokinesis.

A ganglion containing cells which resemble these in form and position are found in the corpora quadrigemina of *Echidna*. This fact gives an additional argument in favour of the theory that the optic lobes of fishes homologize with the corpora quadrigemina of Mammals; as these bodies in *Echidna* are undoubtedly the same as in the Mammalia, so if the former correspond to the optic lobes in fishes, the latter must do so also, since things that are equal to the same are equal to each other.

At the posterior part of the optic lobe there is a problematical body (Pl. XII. fig. 8, *d*) which I have not met with elsewhere; it is situated at the outer and lower edge of the lobe, where it forms a swelling apparently attached to the outer side of the lobe, from which it is distinct. It consists of small spherical cells imbedded in a network with large meshes composed of fibrils; its signification is not apparent, but it appears to be connected with the transverse commissure of the medulla oblongata.

Cerebellum.

The cerebellum (Pl. XIII. fig. 10) has a structure corresponding to that found in Plagiostomata and Teleostei, and, indeed, of the whole vertebrate kingdom.

Four layers are to be distinguished from within outward viz. the fibrous, the granular, intermediate, and molecular.

The fibrous layer consists of nerve-fibres situated close beneath the endothelium; they run obliquely backward and eventually form the crura cerebelli ad medullam; some fibres also of this layer pass through the granular layer; they come up from the internal tuberosity on each side, then turn down along the main lamina of the cerebellum.

The granular layer occupies the space between the fibrous layer and the intermediate; it consists of spherical cells which are imbedded in a loose network of fibrillæ, to which they give off processes.

The intermediate layer, which comprises the Purkinje cells, is conterminous with the molecular layer, to which it might appear to belong; but as these cells send processes not only into the molecular but also into the granular layer, they might be said to belong to both; therefore it is perhaps better to make them into a separate layer, as they are structures characteristic of the cerebellum.

These Purkinje cells, as seen in a horizontal section, have a very irregular shape and give off numerous processes; some have five, four of which go more or less obliquely into the molecular layer, sometimes dividing dichotomously; the fifth in this specimen goes directly into the granular layer. In other cases these cells present a quadrangular form and show four processes, the long axis being placed radially or at right angles to the surface; in these forms two processes pass into the molecular layer and two into the granular; in one case one of the latter processes could be traced into the bundles of the fibrous layer. Other forms also are found, some with three processes and others only with two, the latter being fusiform in shape. The form of these cells in *Ceratodus* does not appear to be fixed, since they vary so much more than is the case in Plagiostomata and Teleostei.

In longitudinal and vertical sections these cells are more often fusiform or take on the shape of an isosceles triangle, which shows that they are more compressed in this direction; in the latter case the apex sends a process into the granular and the base sends two processes into the molecular layer.

At the anterior end of the cerebellum the molecular layer forms a mere cap on the summit of this segment of the brain; but on proceeding further back it is seen to extend laterally over the crura, carrying the other layers with it, but not extending so far over the restiform bodies as in some Plagiostomata; but where the latter become clear of the cerebellum a small piece of the molecular layer is left on their summit, forming a sort of rudimentary resemblance between the two.

The molecular layer shows as its most conspicuous element the processes of the Purkinje cells, which pass towards the outer surface and there form a comparatively coarse network, which in some places gives a diamond-shaped pattern, like cross hatching; this is caused by the terminal branches of the processes dividing dichotomously at their extremities and so obliquely crossing each other; the fibrils resulting from this division are much larger than those which form a minute network, which fills up the intervals between them; the latter have a general tendency to a longitudinal direction, especially well marked towards the outer surface.

In addition to these two sets of fibrillar network there are to be found sparsely scattered through the molecular layer oval and rounded cells, some of which give off processes from their longer axis. The largest measure 23 μ long by 0·0155 millim. wide and their size varies between that and the smaller ones, which are 0·0155 millim. long by 13 μ wide. The spherical cells have the appearance of those found in the granular layer, and have about the same diameter, some being slightly larger. I could not make out that they gave off any processes.

In addition to these there occur also cells of a more elongated type, approaching the fusiform; these measure 24 μ long by 0·0114 millim. broad; they have a large granular nucleus, but no nucleolus can be detected; cells are also seen which form a transition to the oval shape.

Thus there is found in the molecular layer a regular transition from the spherical, passing through the oval, to the fusiform type of cells; the latter give off a process from each end, the one directed towards the outer surface being the thicker of the two and traceable as far as the outer edge, where it may be seen to join the network of the radial processes of the Purkinje cells.

Other cells are to be observed which are situated close to the outer edge; they resemble the oval type; in some places they form a thin layer.

The external surface of the cerebellum is bounded by an epithelium formed of rounded cells, which carry on their external surface flat membranous expansions, corresponding to but more substantial than those found on the inner surface facing the ventricle. This exterior layer of epithelial cells resembles the palissade cells ("Stiftzelle" of Stieda) in the Plagiostomata; but their processes which penetrate the molecular layer are much less marked.

Spinal Cord.

In a section through the spinal cord taken a short distance behind the posterior end of the sinus rhomboidalis the following structures may be distinguished :—

Three pairs of columns in the white substance, viz. the ventral, between the two ventral roots of the spinal nerves, the dorsal, between the two dorsal roots, and the lateral, between the dorsal and ventral roots.

The nerve-fibres of the ventral columns are on an average of a larger size than those of the other two columns; but they do not predominate to such a degree as in the Teleostei. On the other hand, many large-sized fibres are scattered through the lateral columns, which thus show a general average of larger-sized fibres than in Teleostei.

Contrary to what is the case in *Protopterus*, where the grey substance, according to Fulliquet *, repeats exactly the exterior form of the spinal cord, it here has a highly irregular outline. It extends on each side of the central canal in a semilunar form, the concavity being directed downwards; the two ventral horns expand into club-shaped extremities. The dorsal is more irregular in shape, consisting of lamellæ of grey substance, springing from the substantia gelatinosa centralis on each side of the canal and being directed towards the dorsal surface.

The grey substance gradually diminishes in going back until at the posterior end of the cord it nearly disappears.

The concavity of the grey substance coincides with the convexity of the ventral columns, on the summit of which the two multiaxial fibres are imbedded; these occupy a position corresponding to that of the Mauthner's fibres in Teleostei. As far as I can discover, they are distinct from any other kind of nerve-fibre in their structure, but seem to approach nearest to those fibres, of which they appear to be an amplification. They occupy a considerable amount of space on the upper and outer sides of the ventral columns, being conterminous with the lower concave edge of the grey substance on their dorsal sides. They vary in shape in different parts of their course from round to almond-shaped.

The peculiarity of their structure consists in the fact that from forty to fifty axis-cylinders are contained in a single medullary sheath, which is common to all of them. This sheath, notwithstanding its immense extent and thickness, has the appearance and structure of the medullary sheaths of

* *L. c.* p. 41.

ordinary nerve-fibres. The axis-cylinders also resemble those found in other parts of the cord.

Fulliquet *, who appears to have been the first to investigate microscopically the brain of *Protopterus*, describes two large fibres occupying a corresponding position in the spinal cord of that animal; these he terms Mauthner's fibres, but from his plates and the terms in which he mentions them, I should imagine that he refers to Müllerian fibres. The distinction is essential, for while the latter are unprovided with medullary sheaths, the former have them unusually well-developed.

The nerve-fibres of the ventral columns do not so manifestly exceed in size those of the lateral and dorsal columns as they do in Teleostei, consequently they are not so distinctly marked off in *Ceratodus*; the larger ones are accumulated more towards the dorsal edge of the column, those on the ventral side being smaller. There are many larger-sized fibres scattered throughout the lateral columns, while those of the dorsal columns are all of minute dimensions.

The ventral ganglion consists of fibrils, free nuclei, probably connective-tissue cells, and nerve-cells of two kinds; the fibrils pass through in all directions; many are continuous with the fibræ rectæ, which pass down in the central line to the ventral edge of the cord; these latter and many of the others are processes from the endothelial cells which line the central canal.

The nerve-cells are of two kinds: one species, gigantic in size and irregular in shape, is provided with numerous branches; the other smaller, smoother in contour, usually gives off not more than two processes.

The larger species (Pl. XII. fig. 18) are generally placed at the inferior edge of the ventral ganglion; some are elongated and curved, following the outline of the ventral horn of grey substance; they give off two or three processes from each end and four or five from their convex surface, which is inclined towards the white substance, while none are sent off from their concave margin, which embraces the grey substance. These cells are not very numerous; sometimes only one or two are to be seen in a section; these are of the largest size. Occasionally as many as five occur in one section, but never more; in this case they are smaller and are narrow, fusiform, or tripolar, and occupy a position near the edge and also sometimes more in the interior of the ventral horn.

The processes from these cells can be followed for long distances, and can be seen to give off branches, which pass between the trabecular network which forms the supporting

* *L. c.* p. 43.

framework of the cord; some of them can be traced occasionally to the outer edge of the section, where they are found to pass into the longitudinal columns, where they become the finer longitudinal fibres which are to be seen in that position; others can be traced to the centre of the motor tract, where they become the fine fibres which occupy the spaces between the usual larger-sized fibres of the ventral and lateral columns; in most cases these processes of the cells turn backward, in a few they turn forward. In one case I found a process from a cell turning backward in the ventral column and another process from the same cell turning forward in the dorsal part of the lateral column; occasionally a process may be traced into the ventral column of the opposite side of the cord; sometimes a branch is traceable into the substantia gelatinosa centralis, passing dorsad of the multiaxial fibre.

Cells (Pl. XII. fig. 18) with two nuclei are occasionally to be found, each nucleus being provided with a nucleolus; perhaps these cells may be more properly regarded as two distinct cells connected together by a short thick process.

Cells of the other species are found in the substantia gelatinosa centralis, where they form a ganglion corresponding in position to the central ganglion in Teleostei; they are smaller in size and present a smoother and more regular contour than those in the ventral horn; they are flask-shaped or oval, and usually give off one or two processes; their long axis is generally turned towards the dorsal edge. Although no positive connexion could be traced between them and the fibres of the dorsal root, yet the probability is that they unite and that this ganglion belongs to that root. Cells of this species are also found grouped in the fibræ rectæ; one such ganglion is found in this position immediately behind the posterior end of the sinus rhomboidalis. Cells resembling these, but slightly smaller, are occasionally found singly scattered through the field of the ventral columns; they differ, however, in giving off more than one process.

The multiaxial fibres (Pl. XI. fig. 19) commence at the posterior end of the spinal cord and are first met with opposite the hinder end of the abdomen; here they consist of a very few axis-cylinders enclosed in a comparatively small medullary sheath; the axis-cylinders gradually increase in number as the fibres proceed forward, but the increase is not uniform; at about the middle of their course they become much smaller, and after a few sections again enlarge to the original diameter. But this diminution does not occur at the corresponding point on the opposite sides; but the fibre of one side first suffers a diminution, then that of the other side.

Occasionally axis-cylinders may be seen escaping singly or in groups, passing through the medullary sheath, without diminution of size, into the field of the ventral columns. This fact accounts for the diminution of size at various points in the course of the fibres.

The shape of the multiaxial fibres varies according to the part of the spinal cord in which they are observed; at the posterior end they are elliptical, towards the centre they are round, and further forward they are almond-shaped.

Some distance behind its anterior termination (Pl. X. fig. 13) one axis-cylinder has become distinguished from the remainder by its greater consistency, and by its taking the staining-fluid more readily; in some places it becomes clothed with a special medullary sheath, which, however, soon disappears and is not visible in every specimen.

At a short distance posterior to the point where the facial emerges from the brain this axis-cylinder is the only one remaining, all the others having disappeared, the whole fibre having in the meantime gradually diminished in size. The fibre has now quite the appearance of the Mauthner's fibre of the Teleostei, consisting as it does at this point of a single large axis-cylinder surrounded by a thick medullary sheath. Immediately in front of this spot the axis-cylinder of one side decussates with that of the other, the place corresponding with the position of the decussation of the Mauthner's fibres in the Teleostei. After the decussation the two axis-cylinders, still surrounded by the medullary sheath, are to be seen pursuing a course beneath the floor of the fourth ventricle towards the external edge, and can be traced, with the exception of a very small gap, into the root of the facial. Fulliquet * describes a decussation of the fibres which he terms "Mauthner's" at a corresponding place in *Protopterus*; but their destination according to him, although he does not appear to be quite certain on the point, is somewhat different, as he says that they go to the sixth root of the acusticus. While the multiaxial fibre is diminishing in size its place in the ventral column is taken by an increasing number of fibres, which are most probably the axes that have escaped from that body; their destination, as will appear presently, is to form part of the root of the acusticus.

In seeking for the signification of these multiaxial fibres it will be as well to consider what nerve-fibres other nearly-related animals possess. We have in Teleostei the well-known Mauthner's fibres, which occupy a corresponding

* *L. c.* p. 82.

position and which occur also in *Axolotl* *; in these cases the fibres, two in number, have each only one axis-cylinder; but as in *Ceratodus* there are an indefinite number, the homology is not complete; but in *Petromyzon* there are a large number of naked axis-cylinders occupying the ventral columns: these, according to Ahlborn †, are divided into three groups, two median and one lateral, on each side; one fibre of the median group decussates with another of the opposite side at a spot corresponding to where the multiaxial fibre decussates and joins the upper acusticus root; he is not certain about the destination of the remainder of the median group, but the lateral group passes on without decussating and joins the lower acusticus root: thus we have simply to enclose the Müllerian fibres in a medullary sheath and we have the multiaxial fibre; the conclusion is therefore obvious that this fibre is the homologue of the Müllerian fibres of *Petromyzon*.

The ventral columns of the spinal cord pass forward, and spreading out on the ventral edge of the aqueduct of Sylvius, are ultimately lost in the walls of the third ventricle or region of the thalamus; anteriorly they are separated from the crura cerebri by the ventral transverse commissure.

The crura cerebri appear to go principally into the lateral columns or lateral part of the ventral columns; the outer portion of the former furnish the crura cerebelli and also further forward they send fibres into the second layer of the optic lobe.

In the spinal cord the only transverse commissure to be found runs through the substantia gelatinosa immediately above the central canal.

At the posterior end of the medulla oblongata a transverse commissure is seen close to the ventral edge; it first appears in the funnel-shaped backward prolongation of the sinus rhomboidalis, and gradually increases both in lateral and vertical extent; more anteriorly it arrives at its greatest development at the region of exit of the trigeminus group of nerves, the opposite sides of which it serves to connect, as also the region of the vagus. During this course it comes to occupy nearly the whole of the motor tract. But this is not its termination, for it can be traced further forward; at the anterior end of the cerebellum it has become much smaller, but beneath the posterior end of the optic lobe it again increases in size and appears to contribute to the network found in the problematical body (Pl. XII. fig. 8, *d*) on the outer side of the optic lobe;

* Stieda, Zeitschr. f. wiss. Zool. Bd. xxv.
† *L. c.* p. 263.

passing through this body and having arrived at its dorsal end its fibres, or some of them, pass into the optic lobe to join the fibres from the lateral columns of the cord; together they enter the second layer and contribute to form the transverse commissure in the mid line on the dorsal edge of this lobe. The whole seems to correspond to the commissura ansulata of Teleostei.

At and slightly posterior to the exit of the oculomotores this commissure has nearly disappeared, only again to increase in size until it terminates at the posterior end of the *cul-de-sac* which projects a short distance behind the infundibulum; in its course at this part it connects the two sides of the aqueduct of Sylvius, at the part which probably homologizes with the thalamus opticus. This commissure is on the ventral side of the brain; on the dorsal side also there is another commissure, which, commencing at the posterior border of the third ventricle, is continuous backward with the commissure in the roof of the optic lobe; it is the posterior commissure which is found both in Teleostei and Plagiostomata, and corresponds both in position and general arrangement with the posterior commissure in the third ventricle of the Mammalia.

On each side of the fissure on the ventral side of the aqueduct of Sylvius, close behind its entrance into the third ventricle, there is a ganglion containing moderate-sized cells from which a few fibres pass back and ultimately join the anterior prolongations of the ventral columns of the cord.

Deep Origins of the Cranial Nerves.

Optic Nerves.—There is no chiasma nervorum opticorum visible externally, but internally there is at the base of the thalamencephalon a complicated decussation of fibres. Some go from one nerve to the other side, some of the dorsal fibres go from one nerve to the other, but none could be seen to go from the nerve to the optic tract of the same side.

The optic tract passes upward and forward along the external edge of the thalamencephalon until it reaches the optic lobe, where its fibres spread out longitudinally, forming the outer layer of fibres in that structure.

Oculomotores (Pl. XII. fig. 8, *n.* 3).—As Ahlborn has pointed out in *Petromyzon*, this nerve arises from the under surface of the medulla oblongata; although the position of its ganglion is beneath the floor of the aqueduct of Sylvius, yet this is part of the anterior prolongation of the medulla oblongata. In *Ceratodus* it corresponds in position and mode of origin with the same nerve in Teleostei and Plagiostomata.

Patheticus (Pl. XI. fig. 9, *n*. 4).—The trunk of this nerve was not discovered, but that it exists is shown by the fact that its decussation and part of its course and exit is to be seen in the transverse section of the valve of Vieussens, that is to say, in the connecting-link between the cerebellum and the optic lobe.

Trifacial (Pl. X. fig. 11, *n*. 5).—The anterior root of the trifacial is derived from a ganglion situated at the external edge of the floor of the fourth ventricle, where it forms a flat broad swelling, which occupies the space between the ridge of the ventral column and the corpus restiforme; this swelling is visible on macroscopic inspection; from this ganglion the fibres proceed directly downward and outward to emerge at the inferior external angle of the medulla oblongata; it corresponds to the anterior origin in Teleostei, but the root has a more direct course to its exit.

The posterior roots of the trifacial have a single origin, which divides into two trunks immediately outside the brain. The origin is from the tuberosity on the summit of the restiform bodies, constituting part of the continuation of the molecular layer of the cerebellum, which passes on to those bodies where the crura cerebelli are detached; there are here a few medium-sized cells from which its fibres might be derived, but it is principally composed of somewhat coarsely granular neuroglia and numerous fibrils. A bundle of fibres (Pl. XII. fig. 12) from this tuberosity passes down the inner margin of the restiform body, crosses the origin of the facial, and is lost in the field of the medulla oblongata with the transverse commissure which occupies that part.

Facial (Pl. XII. fig. 12, *n*. 7).—This nerve passes into the cord at the inferior external angle in an upward and inward direction until it reaches the angle formed between the floor and the walls of the fourth ventricle, at which point one part of it passes backward as a well-defined bundle in a small tuberosity, in which it can be traced backward for a long distance, and is eventually lost in the grey matter of the tuberosity at about the middle of the ventricles.

The remainder of this nerve has a more direct origin from the grey matter of the lower part of the wall of the ventricle, beyond which this part cannot be traced.

Acusticus (Pl. XII. fig. 12, *n*. 8).—This nerve, arising below the facial, passes obliquely upward and inward until it reaches the floor of the fourth ventricle at a point some distance internal to the facial. On attaining the grey matter of the floor of the ventricle ("Bodengrau" of German authors) it turns towards the mid line until it arrives at the margin of the ventral column, running close beneath the endothelial lining of the floor; arrived at the summit of the ventral columns, it appears to turn back, and is traceable for some distance as a bundle of fibres smaller than the remainder, which I have reason to believe become part of the multiaxial fibre; in its course along the floor this nerve traverses a collection of cells from which some of its fibres may be derived.

Vagus (Pl. XII. fig. 14, *n*. 11).—The first root arises from the outer angle of the medulla oblongata at some distance behind the exit of the acusticus, but at a slightly higher level; it passes into the floor of the ventricle, where it enters the tuberosity which contains the tract of the facial; the tuberosity enlarges for its reception; it then passes back close to the outer side of that tract. After the disappearance of the facial the tuberosity becomes larger and is composed of finely granular neuroglia; the dorsal part is occupied by cells in which the bundle in question disappears.

This tuberosity extends nearly to the posterior end of the fourth ventricle and receives in succession the remaining roots of the vagus, which are all derived from the same origin; it is continuous, and not discrete, as in *Scyllium* and *Acanthias*. There are five roots discernible, the three posterior of which are double, although the external nerve resulting is single; this would make the trunk of the vagus equivalent to eight nerves. All these roots are dorsal, and in this species there are no ventral roots. Behind the last root of the vagus two nerves are given off which have only ventral roots; they arise in precisely the same way as the ventral roots of the spinal nerves, the only difference being that they have each two roots in the medulla oblongata. In *Ceratodus* at least they do not belong to the vagus.

Spinal Nerves.—The dorsal roots enter the spinal cord at a point close to the mid line, but they diverge as they pursue their course through the parenchyma, so that in the interior of the cord they are further from the central line than they are at their point of emergence. The individual fibres are of a large size, equalling those of the ventral root. The entering fibres turn forward in the substance of the cord, immediately outside the grey substance of the dorsal horn.

The ventral roots, after entering the cord, follow a forward and upward course towards the inner edge of the multiaxial fibre, usually passing between that fibre and the central canal over its dorsal edge; they are lost in the grey matter at its outer angle. Sometimes a fibre belonging to this root may be traced, after having followed the path above mentioned in a longitudinal direction, into one of the fibres of the ventral column situated between the outer edge of the multiaxial fibre and the ventral horn of grey substance. In one case a fibre from the ventral root was seen to join a process from one of the large ventral ganglion-cells after having followed a similar course.

Conclusion.

As far as the brain is concerned *Ceratodus*, as Prof. Huxley has already remarked, holds a somewhat central position.

This animal having such an archaic form and differing so little from its predecessors of the Carboniferous epoch in structure, it is interesting to note the embryonic condition of its brain, as shown in three points:—first, the extreme size of its ventricles, which are surrounded by a very thin layer of nervous tissue; second, the alternating dorsal and ventral roots of the spinal nerves; and third, the origin of the dorsal roots of the spinal nerves in close proximity to the central line.

Ceratodus presents points of contact with all the principal divisions of the class, and it does not appear to approximate more to its nearest congener, *Protopterus*, as far as the brain is concerned than to other members of its class. While it differs from *Protopterus* in the shape and imperfection of its cerebral lobes, it agrees in the general contour and in the narrowness of the mesencephalon and the breadth of the medulla oblongata, as also in the rudimentary character of the cerebellum, which is a mere bridge over the sinus rhomboidalis, although it is much larger in *Ceratodus* than in *Protopterus*. The former also differs in having a well-developed olfactory lobe, which is not present as a distinct structure in *Protopterus*.

With regard to the other orders of this class *Ceratodus* agrees with the Ganoids in the comparative narrowness of the mesencephalon and thalamencephalon and the proportions of the cerebellum.

With the Plagiostomata it agrees in the structure of the optic lobes and in the size and mode of attachment of the olfactory lobes to the cerebrum, a fact which was shown by Prof. Huxley. It can scarcely be said that they agree in the structure of the prosencephalon, since in the Plagiostomata the ventricles are perfect and the nervous tissue well developed, whereas in *Ceratodus* the ventricles are imperfect and the nervous tissue scanty.

With the Teleostei the only point of contact appears to be the multiaxial fibres, although these present a large measure of dissimilarity in the greater part of their course; yet at their anterior end they show a similarity both in their appearance when only one axis-cylinder remains enclosed in the medullary sheath, and also in the fact of their decussation and in the position of that decussation.

With *Petromyzon* the only points of contact are the tela choroidea, which covers in the fourth ventricle, and the multiaxial fibre; the tela choroidea appears to have the same sort of structure, and if my supposition be correct the multiaxial fibre represents a more advanced stage of development of the Müllerian fibres.

With regard to the other division of the class Ichthyopsida, viz. the Amphibia, there seem to be as many points of difference as agreement, so that from the point of view of the structure of the nervous system *Ceratodus* appears to be quite isolated, and while presenting some agreement in structure with all the members of the class Pisces, is nearly related to no one of them.

EXPLANATION OF PLATES VIII.–XIII.

The following letters have the same signification throughout:—

a. c. Anterior commissure.
aq. sy. Aqueduct of Sylvius.
b. Nervi branchiales.
b. ce. Inferior bulla of the cerebrum.
c. a. Commissura ansulata.
c. c. Crura cerebri.
c. ca. Central canal of the spinal cord.
c. cbl. Crura cerebelli ad medullam.
cbl. Cerebellum.
ce. Cerebral lobes.
c. g. Cells of the central ganglion.
ch. op. Chiasma nervorum opticorum.
ch. te. Tela choroidea.
co. Communicating branch between the trifacial and the vagus.
co. p. Communicating branch between the glossopharyngeal and vagus ganglion.
c. v. g. Cells of the ventral ganglion.
d. h. Dorsal horn of the grey substance.
d. l. Dorsal longitudinal columns.
d. r. Dorsal roots of the spinal nerves.
e. Epiphysis.
f. a. Fibres belonging to the acusticus.
f. f. Fasciculus of the root of the facial nerve.
f. l. Fibrous layer of the cerebellum.
g. l. Granular layer of the cerebellum.
gl. o. Glomeruli olfactorii.
gn. h. Ganglion Habenulæ or tuberculum intermedium.
gn. r. op. Ganglion of the roof of the optic lobe.
gn. th. Ganglion of the thalamencephalon.
gn. tri. Ganglion of the trifacial.
gn. v. Ganglion of the vagus.
i. l. Internal layer of the olfactory lobe.
i. m. Inferior maxillary nerve.
in. Infundibulum.
l. c. Lateral columns of the cord.
m. Combined superior and inferior maxillary nerve.
m. ce. Mesencephalon.
m. l. Molecular layer of the cerebellum.
mlt. Multiaxial fibre.

m. ob. Medulla oblongata.
m. th. Mesethmoid cartilage.
n. 2. Optic nerves.
n. 3. Oculomotor nerves.
n. 4. Trochleares nerves.
n. 5. Trifacial nerves.
n. 7. Facial nerves.
n. 8. Acusticus.
n. 9. Glossopharyngeal.
n. 10. Vagus.
o. Ophthalmic nerve.
ol. o. Olfactory sac.
op. l. Optic lobe.
op. tr. Optic tract.
pa. Palatine nerve.
p. c. Posterior commissure.
pi. Hypophysis cerebri.
p. m. Pia mater.
p. p. Process of the pterygopalatine bone.
pr. Prosencephalon.
r. c. Restiform column.
rh. Rhinencephalon.
r. i. Ramus intestinalis.
r. l. Ramus lateralis.
s. g. c. Substantia gelatinosa centralis.
sp. gn. Spinal ganglion.
sp. n. Spinal nerve.
s. r. Sinus rhomboidalis or fourth ventricle.
t. c. op. Transverse commissure of the optic lobe.
th. Thalamencephalon.
t. i. Tuberculum intermedium.
t. tri. Tuberosity of the trifacial.
t. v. Tuberosity of the vagus.
v. c. Ventriculus communis.
v. h. g. Ventral horn of grey substance.
v. l. c. Ventral longitudinal column.
v. r. Ventral roots of the spinal nerves.
v. t. c. Ventral transverse commissure.
v. th. Third ventricle.
v. v. Valve of Vieussens, valvula cerebelli, or anterior medullary velum.

Fig. 1. Dorsal view of the brain, with the distribution of the nerves, as far as can be seen on that aspect; right side shows the superficial nerves, left side the deeper nerves, natural size.
Fig. 2. Side view of the brain, with part of the skull in outline, nat. size.
Fig. 3. View of the brain from below, nat. size.

[Transverse sections arranged in consecutive order from before backward.]

Fig. 4. Transverse section through the prosencephalon immediately behind the point where the two sides become entirely separated from each other, $\times\ 6\frac{1}{2}$.
Fig. 5. Transverse section through the anterior part of the thalamencephalon with the chiasma of the optic nerves and the crura cerebri, $\times\ 8\frac{1}{2}$.
Fig. 6. Transverse section through the posterior end of the thalamencephalon and the infundibulum, $\times\ 8\frac{1}{2}$.
Fig. 7. Transverse section through the anterior end of the aqueduct of Sylvius, at the point where the infundibulum becomes clear of the inferior surface of the brain, $\times\ 8\frac{1}{2}$.
Fig. 8. Transverse section through the mesencephalon at the point where the oculomotores emerge, $\times$ 14.
Fig. 9. Transverse section through the valve of Vieussens, showing decussation of the fourth nerve and posterior edge of the optic lobe, $\times$ 14.
Fig. 10. Transverse section through the cerebellum, $\times$ 14.
Fig. 11. Transverse section through the origin of the anterior root of the trifacial nerve, $\times$ 14.
Fig. 12. Transverse section through the sinus rhomboidalis at the point of apparent origin of the posterior root of the trifacial, facial, and acusticus, $\times$ 14.

Fig. 13. Transverse section through the sinus rhomboidalis at the point where the multiaxial fibre decussates.
Fig. 14. Transverse section through the sinus rhomboidalis at the apparent origin of the vagus, × 14.
Fig. 15. Transverse section through the spinal cord a short distance behind the fourth ventricle. Some of the detail was added from another specimen. × 24.
Fig. 16. Transverse section through the middle portion of the spinal cord, × 24.
Fig. 17. Transverse section through the posterior part of the spinal cord, × 24.
Fig. 18. Two cells from the ventral ganglion of the cord: *v*, the side turned towards the ventral edge; *d*, the side turned towards the dorsal edge; the grey substance of the ventral horn is situated between the two on the concave side of the upper and on the convex side of the lower cell. × 65.
Fig. 19. Section through the multiaxial fibre: *m. s.*, medullary sheath; *a. c.*, axis-cylinders; *b*, the axis-cylinder destined to decussate. × 120.
Fig. 20. Cells from the roof-ganglion of the optic lobe, × 180.
Fig. 21. Transverse section through the olfactory lobe, × 180.
Fig. 22. Longitudinal and vertical section through the dorsal part of the cerebrum, × 180.
Fig. 23. Transverse section through the optic lobe, × 180.

XIX.—*New Genera and Species of* Trichopterygidæ. By Rev. A. Matthews.

The Trichopterygidæ have numerically increased to such an extent since the publication of the 'Trichopterygia Illustrata' in 1872, that I have for some time contemplated adding a second part to that work. Many of the new species have been already described in various periodical and other works, but some few still remain unnoticed. And since the publication of a more comprehensive work has hitherto been, and may yet be, retarded by causes over which I have no control, I propose in the following pages to give a short summary of their chief distinctive characters, reserving more detailed descriptions to some future period.

The two new genera described in this paper are both of a most extraordinary and novel character, and extremely elegant in form. In *Mikado* the front of the head is produced into an elongated snout or rostrum, after the manner of some species of *Rhinosimus*; but this part is deflexed, and, when at rest, laid upon the prosternum, so that, if viewed from above, the head presents the appearance usual to *Trichopteryx*. In *Dimorphella*, as its name implies, the sexes would appear